Life imitates op art

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The beautiful, undulating orientation maps in visual cortex have motivated many developmental models. A new study finds that this functional organization could be seeded in the retina by moiré interference between mosaics of ON-center and OFF-center retinal ganglion cells.

Moiré interference occurs when two periodic structures are superimposed such that a new spatial structure emerges (**Fig. 1a**), an effect that is exploited in the works of op artists such as Carlos Cruz-Diez and Ludwig Wilding (**Fig. 1b**). In this issue, Paik and Ringach[1] demonstrate how moiré interference can account for the architecture of orientation maps (**Fig. 1c**). The underlying periodic structures are the evenly spaced mosaics of ON and OFF retinal ganglion cells, and the orientation map is a result of the relative positions of these two superimposed mosaics.

The visual cortex has maps for different features of visual stimuli, including ocular dominance, orientation and spatial frequency. The ocular dominance map was the first of these to be imaged. In 1974, Wiesel, Hubel and Lam injected radioactive tracers into one eye, which were transported trans-synaptically to the visual cortex. They then sectioned the radioactive cortex and used it to expose photographic film, revealing the characteristic stripes of ocular dominance[2]. This approach was possible because of the clear anatomical origin of the cells whose outputs segregate into ocular dominance columns: the left and right retinas. Imaging orientation maps, however, was a bit trickier. It took *in vivo* imaging to capture their structure. The orientation map was first imaged by Blasdel and Salama[3] (**Fig. 1c**). These striking, multicolored images ignited the imaginations of neuroscientists everywhere. How can neural circuitry develop such a complex architecture for orientation maps? The answer may lie in pure geometry, and like the ocular dominance map, it too may emerge at the level of the retina.

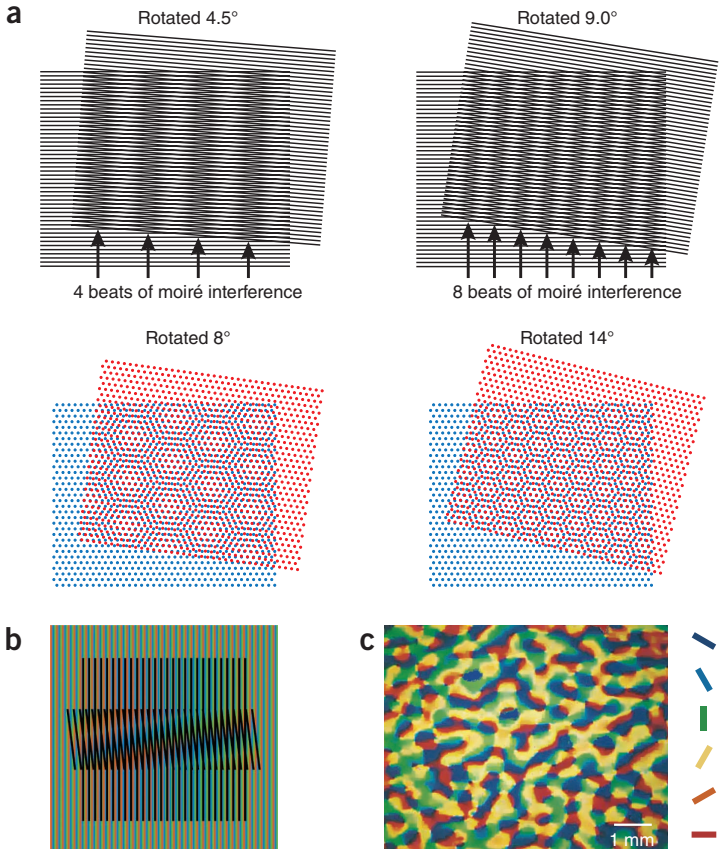

Figure 1 Moiré interference, retinal ganglion cell mosaics and orientation maps. Moiré interference occurs when periodic patterns are superimposed and slightly rotated relative to each other. The effect manifests as a new periodic pattern that repeats on a spatial scale larger than that of the underlying component patterns. (**a**) Top, this is easily observed with two horizontal line gratings. The spatial scale of the beats in the moiré interference pattern change depending on the relative orientation of the two underlying patterns. Bottom, in the retina, ganglion cell receptive fields are arranged in hexagonal lattices called mosaics. Each type of retinal ganglion cell is arranged in its own mosaic. Moiré interference patterns in the superposition of these two mosaics are visible with this pattern as well. (**b**) Moiré patterns in op art: Carlos Cruz-Diez, *Induction Chromatique*, Paris, France, 2007, 100 × 100 cm, © Cruz-Diez Foundation. (**c**) Orientation columns in primate visual cortex, as first reported by Blasdel and Salama[3], may be seeded by moiré interference between two different retinal ganglion cell mosaics, one for ON retinal ganglion cells and one for OFF. Image is taken from reference 3.

This provocative idea obviates the need for activity-dependent plasticity, a feature present in many models of the development of orientation maps.

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Paik and Ringach[1] started with a topological model of visual system wiring in which postsynaptic neurons are most likely to synapse with the retinotopically nearest presynaptic afferents, and synapse with more distant afferents with a probability and strength that decrease with distance[4]. Because the ON retinal ganglion cells are each evenly spaced amongst themselves in a mosaic, as are the OFF cells, the nearest neighbor for an ON cell is typically an OFF cell, and vice versa, owing to a positional shift between the two mosaics. These neighboring ON and OFF retinal ganglion cells form dipoles and define the local orientation tuning bias. If the positional shift between the two mosaics is consistent over the retina and can be characterized by a particular rotation and/or difference in cell density, then the superposition of the two retinal ganglion cell mosaics yields a moiré interference pattern.

Paik and Ringach[1] found that the relative angle and periods of the two mosaics, summarized in a scaling factor *S*, create different spatial patterns of dipoles and greatly influence the resulting orientation maps in the model. By picking appropriate values for *S*, they produced orientation maps with characteristics that were similar to those of various species, from primates to rodents. A telltale feature of the maps generated by the model provided a key test. In model-generated maps, iso-orientation domain centers were arranged in a hexagonal lattice. When real orientation maps were examined for this feature, such geometric patterns were clearly evident in maps from all four of the species tested. Furthermore, control orientation maps, which were computationally generated to have an isotropic spatial frequency profile, did not exhibit this hexagonal arrangement of iso-orientation domains. Using published data for the monkey *Macaca fascicularis*, the authors estimated the relative rotations for ON and OFF retinal ganglion cells to be around 5 degrees. This implies that the two mosaics are not entirely independent and predicts that there are molecular mechanisms to ensure specific relative rotations of ON and OFF retinal ganglion cell mosaics.

The key features of this model are resistant to physiological levels of noise. However, detection of the moiré interference patterns by eye can break down quickly with increasing noise. In fact, it was only when the authors explored the noise-free version of the model that its basis in moiré interference became apparent.

The idea that retinal mosaics themselves could seed architecture in visual cortex has been pondered since at least 1981 (ref. 5). Five years later, the idea was formally modeled by Soodak[6], and recently the model has been explored in more depth and generalized[4,7]. In the past year, new experimental data supporting the hypothesis has emerged.

The model used in this work relies on an important assumption: neurons in visual cortex are primarily driven by a pool of afferents with fairly limited diversity[4]. That is, neurons in visual cortex don't have much to choose from when connecting to their bottom-up inputs, and the limited pool that is available imposes an orientation bias, which arises from the dipoles created between ON and OFF retinal ganglion cells. Data supporting this idea in the cat visual system have recently been reported. Simultaneous recordings in the thalamus and visual cortex indicate that the receptive fields of the thalamic afferents in a local region of visual cortex show low scatter, and the coverage of ON and OFF receptive fields is unequal. This limited diversity predicts the local orientation tuning in visual cortex[8].

This principle of limited afferent diversity seems to hold even in mice, which lack orientation maps. Local populations of mouse visual cortex neurons exhibit a small number of unique ON and OFF receptive field subregions, which are integrated in different combinations by individual neurons[9]. Thus, this principle of a limited diversity of bottom-up inputs may be a general one. But why then do rodents not have orientation maps? The lack of orientation maps in a highly visual rodent, the squirrel, rules out the possibility that visual acuity or the size of visual cortical area are the limiting factors[10]. Paik and Ringach[1] suggest that a small scaling factor may be the reason why rodents lack an orientation map. However, they note that many factors may contribute to the breakdown of the moiré interference pattern, including positional noise in the mosaics.

Not only does the model account for the variations in orientation maps from species to species, it also accounts for the observation of well-tuned neurons in the absence of smooth maps and for the breakdown of the map in foveal regions. This simple, parsimonious model reproduces a great many features of orientation maps and does not invoke any kind of activity-dependent plasticity, such as spike timing–dependent plasticity or Hebbian plasticity, which is a key feature of many other developmental models[11].

This is not to say that the model rules out a role for activity-dependent plasticity in the development of cortical architecture. For example, the limited pool of afferents, which is so essential for the model and is supported by experimental findings in adult animals, may at least partially arise from activity-dependent mechanisms. In particular, developmental pruning of extra inputs at the retino-geniculate synapse may be activity dependent and pave the way for the later seeding of orientation columns in visual cortex. Furthermore, later developmental processes, such as matching the orientation maps for the two eyes, are activity dependent[12]. Nevertheless, the activity independence of this model is attractive in that it offers an explanation as to why visually inexperienced animals have orientation maps[13].

This is not the first appearance of moiré interference in recent biomedical research. It has been invoked in the interference model of hippocampal grid cell firing and there it offers a degree of scale invariance[14]. In addition, it is the basis for an elegant method of wide-field microscopic imaging that offers resolution beyond the classical Abbe diffraction limit[15]. This op art trick has turned out to be a surprisingly powerful computational tool.

The work by Paik and Ringach[1] shows how statistical wiring mechanisms, combined with evenly spaced mosaics of retinal ganglion cells, can give rise to surprisingly sophisticated neural architecture in visual cortex. It will be interesting to see how general these concepts turn out to be. Are there other portions of cortical architecture that are seeded by a superposition of periodically arranged afferents? Do other neural circuits show similar statistical wiring and low degrees of diversity in their afferents? These are questions motivated by the striking success of this simple, parsimonious model.

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

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